Cellular Organization and Regulation of Plant Glycerolipid Metabolism

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Great strides have been made in understanding how membranes and lipid droplets are formed and maintained in land plants, yet much more is to be learned given the complexity of plant lipid metabolism. A complicating factor is the multi-organellar presence of biosynthetic enzymes and unique compositional requirements of different membrane systems. This necessitates a rich network of transporters and transport mechanisms that supply fatty acids, membrane lipids and storage lipids to their final cellular destination. Though we know a large number of the biosynthetic enzymes involved in lipid biosynthesis and a few transport proteins, the regulatory mechanisms, in particular, coordinating expression and/or activity of the majority remain yet to be described. Plants undergoing stress alter their membranes' compositions, and lipids such as phosphatidic acid have been implicated in stress signaling. Additionally, lipid metabolism in chloroplasts supplies precursors for jasmonic acid (JA) biosynthesis, and perturbations in lipid homeostasis has consequences on JA signaling. In this review, several aspects of plant lipid metabolism are discussed that are currently under investigation: cellular transport of lipids, regulation of lipid biosynthesis, roles of lipids in stress signaling, and lastly the structural and oligomeric states of lipid enzymes.

Keywords: Membrane • Lipids • Lipid transport.

Introduction

Lipid metabolism in plants is an essential process that provides cells with membranes, a storage form of energy and building blocks, and potent signaling compounds. In this review, we will give some necessary background on plant lipid metabolism and outline the frontiers of our knowledge on plant lipid biosynthesis and transport. In addition, we will point out the outstanding questions about the biophysical arrangement or topology of lipid biosynthetic enzymes. Plant cells, as any other eukaryotic cell, are composed of many membrane systems and compartments with unique lipid compositions. Here, we will focus primarily on land plants and how they carry out lipid biosynthesis in the plastid and the endoplasmic reticulum (ER), and related processes associated with those compartments. Most of the information described here is based on

the model plant *Arabidopsis thaliana* (*Arabidopsis*) unless otherwise indicated.

In both the ER and plastid, phosphatidic acid (PA) is the first lipid species formed by de novo complete acylation of glycerol-3-phosphate (glycerol-3-P). During the biosynthesis of PA, the specificity of the acyltransferases associated with the respective compartments determines the length of acyl chains esterified. In the plastid, glycerol-3-P acyl transferase and lysophosphatidic acid acyltransferase (ATS1 and ATS2) produce a PA bearing 18:1 and 16:0 acyl chains (carbon #: double bond #) at the *sn*-1 and *sn*-2 positions of the glycerol backbone, respectively (Bin et al. 2004, Kim and Huang 2004, Tzafrir et al. 2004, Xu et al. 2006). Meanwhile, the ER acyltransferases produce a PA with predominantly 18-carbon acyl chains at both *sn*-1 and *sn*-2 positions (Kim et al. 2005). This distinction results in two identifiable sets of molecular species of lipids that are, within limitations, representative of the lipid assembly in the respective compartments. Though the fluxes through these two parallel pathways have been estimated based on the 16/18 carbon ratio, or more precisely by positional analysis of membrane lipid acyl composition, there are some caveats on the specificity of acyltransferases and possible lipid reassembly. For example, acyl editing of chloroplast-assembled lipids has recently been observed through in vivo lipid tagging using an ER-targeted $\Delta 6$ -desaturase from *Physcomitrella patens* (Hurlock et al. 2018). Already, acyl editing of ER lipids has been known for some time for phosphatidylcholine (PC) in plants (Bates et al. 2007). However, if acyl editing of chloroplast lipids contributes significantly to the acyl composition of chloroplast lipids, the reliability of the 16/18 carbon ratio as a simple metric for the origin of plastid lipids needs to be reevaluated. This is particularly true for *Chlamydomonas*, for which a plastid-type lysophosphatidic acid acyltransferase associated with the ER has been discovered (Kim et al. 2018), explaining the unusually high 16/18 ratio of *Chlamydomonas* galactolipids, even though it has been shown to import ER-derived lipid precursors into the plastid (Warakanont et al. 2015).

In addition to differing acyltransferase preferences of the two pathways, the conversion of PA to other lipid classes also differs between the two compartments as the ER produces exclusively phospholipids and triacylglycerols while the plastid synthesizes the phospholipid phosphatidylglycerol (PG), the sulfolipid sulfoquinovosyldiacylglycerol (SQDG), and the two

galactolipids mono- and digalactosyldiacylglycerol (MGDG and DGDG).

Though components of both pathways are present in most land plants, not all plants utilize them both or to the same extent. For example, grasses primarily rely on the ER pathway (Petroutsos et al. 2014, Yang et al. 2017). However, to understand the interplay between the ER and plastid pathways, *Arabidopsis* provides an excellent starting model due to its near equal utilization of both pathways.

Lipid Transport Mechanisms

As pointed out above, *Arabidopsis* produces glycerolipids through the plastid and ER pathways, also denoted prokaryotic and eukaryotic pathways, respectively (Browse et al. 1986, Kunst et al. 1988, Mongrand et al. 1998). There is also some lipid assembly in the mitochondrion and the reader is directed to the Acyl-Lipid Metabolism chapter of the *Arabidopsis* Book (Li-Beisson et al. 2013) for further information concerning mitochondrial lipid metabolism. Though the assembly of glycerolipids occurs in more than one compartment, with the exception of fatty acids synthesized in the mitochondrion mostly as precursors to lipoic acid (Wada et al. 1997), the plastid is the location where the vast majority of fatty acids are de novo synthesized. In order to supply substrates to the glycerolipid assembly machinery at the ER, acyl groups must be exported from the plastid. In addition, the ER provides glycerolipid precursors to the chloroplast requiring a transport system. The flux of acyl groups from the plastid is substantial especially in seed oil storage tissues, and yet at this time it is still not unambiguously known by which molecular mechanism the acyl groups are exported from the plastid (Fig. 1) (Koo et al. 2004). One hypothesis suggests transport of lipids or fatty acids through ER-plastid contact sites, which have been observed (Andersson et al. 2007). An inner chloroplast envelope membrane-spanning protein FAX1 seems to play a role in lipid homeostasis of ER-derived lipids and can complement the *fat1* yeast mutant deficient in fatty acid export (Li et al. 2015). Although FAX1 is likely to aid in the transport of fatty acids across the inner envelope membrane (IEM) at least in specific tissues, it appears as though not all fatty acid export from chloroplasts is abolished in the *fax1* mutant and other mechanisms may be in play. The necessity of transport channels or other protein-mediated mechanisms to move fatty acids across the IEM as well as the outer envelope leaflets to the ER membranes (Fig. 1) makes this an active area of research.

After lipids are assembled at the ER, there are several proposed mechanisms on how those lipids make it back to the plastid. One reported transport mechanism involves the phospholipid transporter ALA10. Mutants of ALA10 have a lowered MGDG/PC ratio and ALA10 overexpression leads to an increase in MGDG/PC ratio, suggesting a role of ALA10 in maintaining MGDG metabolism in the chloroplast (Botella et al. 2016, Botella et al. 2017). Based on these data, it was concluded that this transporter may be important for efficient translocation of PC across the ER membrane and to the plastid

Fig. 1 Scheme of PA synthesis in the plastid and the ER. Denoted with letters are outstanding transport mechanisms proposed and yet to be characterized: the unknown exporter of acyl groups across the outer envelope membrane (OEM) of the plastid (A) and the transport mechanism by which plastid-assembled PA is moved through the IEM of the plastid (B). FAS, fatty acid synthesis; FAX1, fatty acid exporter 1; GPAT, glycerol-3-P acyltransferase; LPAT, lyso-phosphatidate acyltransferase; TGD 1, 2, 3, 4, 5, trigalactosyldiacylglycerol 1, 2, 3, 4, 5.

either through ER-plastid contact sites or by another mechanism yet to be described.

A means of reimporting ER-assembled lipids into the plastid has been described and a multiprotein ABC transporter complex consisting of three proteins TRIGALACTOSYLDIACYLGLYCEROL1, 2, 3 (TGD1, 2, 3) has been identified. Together with two additional proteins, TGD4 and TGD5, these proteins provide a conduit for lipid transfer that spans the outer and IEMs of the plastid and coordinates lipid import from the ER in a unidirectional manner (Xu et al. 2003, Xu et al. 2005, Awai et al. 2006, Lu et al. 2007, Lu and Benning 2009, Xu et al. 2010, Roston et al. 2011, Roston et al. 2012, Fan et al. 2015). TGD4 and TGD5 are located at the outer envelope, where TGD4 contains a PA binding site (Wang et al. 2013) and is hypothesized to facilitate the translocation of ER-assembled PA to the plastid membranes (Wang et al. 2012). This occurs in coordination with the inner envelope subcomplex composed of TGD1, TGD2 and TGD3, which may also assist the translocation of PA through the identified PA-binding site of the TGD2 protein (Awai et al. 2006, Lu and Benning 2009). Since PA is also synthesized at the chloroplast stroma side of the IEM, there could be an outwards transporting mechanism that translocates plastid PA and inserts it into the same leaflet as the ER-sourced PA. A bacterial ABC transporter of lipopolysaccharide (LPS) precursors resembling the plant TGD complex has been shown to mediate the outwards transport of lipids from the inner membrane to the outer membrane of the cell (Sperandeo et al. 2008). Bacterial lipid transporter systems Mla, Pqi and Yeb, have been structurally analyzed and have intermembrane spanning projections, like the LPS transporter and the TGD complex, which aid in lipid transport from the inner to the outer membrane (Ekiert et al. 2017). It is possible that similar mechanisms exist to move plastid-assembled lipids outwards through the chloroplast to the envelope membranes (Fig. 1).

As both eukaryotic and prokaryotic DAG species are galactosylated by monogalactosyldiacylglycerol synthase 1 (MGD1) located at the intermembrane leaflet of the IEM, the transport of the product MGDG to the thylakoid membranes (THY) needs to be aided by a protein channel or transport mechanism. In addition to MGDG, the product of digalactosyldiacylglycerol synthase 1 (DGD1), DGDG, must also be translocated across the outer and IEMs to be incorporated into the THY. These galactolipid transport mechanisms could share the same machinery or use specific transporters for each lipid (Fig. 2). A proposed mechanism by which DGDG moves from the outer envelope to the IEM involves the N-terminal extension of DGD1 itself (Kelly et al. 2016) (Fig. 2).

Another intriguing area of study is the export of plastid lipids under certain environmental stresses such as phosphate starvation. A study looking for a non-DGD1 dependent pathway of DGDG synthesis led to the discovery of a suppressor mutant *dgs1* which accumulates galactolipids despite lacking the enzyme DGD1 responsible for the bulk synthesis of DGDG (Xu et al. 2008, Moellering and Benning 2010). Interestingly, the homozygous *dgd1/dgs1* mutant also accumulated oligogalactolipids (Xu et al. 2008) such as TGDG which are typically induced by freezing stress (Moellering et al. 2010). Under phosphate starvation, Arabidopsis plants substitute phospholipids for galactolipids in order to maintain cellular membranes while reserving phosphate for DNA and protein synthesis (Härtel et al. 2000, Härtel et al. 2001, Kobayashi et al. 2009). During early stages of phosphate starvation, PC abundance, unlike other phospholipids, increases and so does DAG that may be derived from the PC before glycolipid synthesis increases (Jouhet et al. 2003). There is some evidence that a mitochondrial complex containing Mic60 plays a role in the response to phosphate starvation and import of plastid-derived galactolipids to the mitochondrion under phosphate starvation (Michaud et al. 2016). It is also hypothesized that MGDG is important during pollen tube expansion to satisfy the need for lipids for rapidly growing membranes (Kobayashi et al. 2004). Galactolipids like DGDG can be detected by antibody in the plasma membrane and the abundance of MGD synthases 2 and 3 is high in pollen tubes. The use of a synthetic MGD

synthase inhibitor galvestine-1 showed reduced pollen tube elongation (Botte et al. 2011). These are a few examples of the presence of galactolipids in extraplastidic membranes requiring export from the plastid. Presumably, the ER as well as other cellular membranes would acquire galactolipids by mechanism similar to those apparent during phosphate-deprived conditions.

Regulation of Lipid Metabolism

For an integral process such as membrane biogenesis, there must be tight regulation of the flux through the lipid biosynthetic pathways. However, surprisingly little is known about the means by which lipid-synthesizing enzymes are regulated with regard to their genes' expression or their enzymatic activity. One of the better understood regulatory mechanism of lipid metabolism is the regulation of the heteromeric acetyl-CoA carboxylase (ACCase), the complex initiating fatty acid synthesis within plastids. The expression of ACCase subunit genes is coordinated, and it appears that the amount of each subunit is modified post-translationally as subunits oligomerize and excess proteins are degraded (Sasaki and Nagano 2004), and the protein activity is stimulated by light (Sasaki et al. 1997). Like in animals and yeast, plant ACCase enzymes in Arabidopsis, Nicotiana and Brassica, have been shown to catalyze the committed step of fatty acid synthesis, and respond to feedback inhibition by fatty acids (Shintani and Ohlrogge 1995, Andre et al. 2012, Bates et al. 2014). Negative regulators of the ACCase in Arabidopsis, BAD1, 2 and 3, have been proposed to function in a competitive manner to inhibit the activity of the heteromeric ACCase (Salie et al. 2016, Keereetawee et al. 2018).

Another manner of controlling lipid biosynthesis involves the WRINKLED1 (WRI1) transcription factor, which regulates the rate of acyl chain biosynthesis. Several WRI isoforms have been characterized, but their functions seem dependent on their tissue/cell-specific presence. WRI1 stimulates the production of fatty acids, and ectopic expression of *WRI1* leads to more oil accumulation in Arabidopsis seeds and seedlings grown on sucrose media (Cernac and Benning 2004). While *WRI1* expression is associated with seeds, *WRI3* and *4* activity was narrowed to floral tissues, where *WRI4* promoter-beta-glucuronidase (GUS) fusion-staining also appeared to be present in plant nectaries (To et al. 2012). In seed tissues, *WRI1* also controls the expression levels of *BCCP2* and thereby ACCase and fatty acid synthesis (Thelen et al. 2001, Ruuska et al. 2002). *WRI1* orthologues have been found in different oil storing tissues, e.g. the embryo in maize (*Zea mays*), the mesocarp in oil palm (*Elaeis guineensis*) (Pouvreau et al. 2011, Ma et al. 2013), castor bean (*Ricinus communis*), rapeseed (*Brassica napus*), nasturtium (*Tropaeolum majus*), the burning bush (*Euonymus alatus*) (Troncoso-Ponce et al. 2011) and non-seed tissues of Chinese tallow (*Triadica sebifera*) (Divi et al. 2015). The regulatory nature of *WRI1* transcription factors has made them prominent targets for the engineering of oil content in different tissues (Reynolds et al. 2015, Yang et al. 2015). *WRI1* alone is not fully capable of turning on triacylglycerol (TAG)

Fig. 2 Proposed movement of galactolipids after synthesis from diacylglycerol (DAG). Denoted with letters are the unknown mechanisms of transport of MGDG and DGDG (A and B, respectively) to the THY, after synthesis by MGDG synthase 1 (MGD1) at the IEM and DGDG synthase 1 (DGD1) at the outer envelope membrane (OEM). PAP, phosphatidic acid phosphatase.

biosynthesis, but when co-produced with a diacylglycerol acyl-transferase (DGAT), *Nicotiana benthamiana* leaves were able to achieve higher levels of TAG accumulation than that with WRI1 production alone (Vanhercke et al. 2013). Increases in oil content of Arabidopsis by ectopic production of WRI1 and suppression of starch synthesis resulted in increases of oils in vegetative tissues (Sanjaya et al. 2011). Combining WRI1, DGAT1 and OLE1 ectopic production, while also abolishing sucrose export from leaves and starch synthesis, pushed the flux of carbon to TAG storage even more (Zhai et al. 2017b). In sugarcane, overexpression of *WRI1* resulted in doubling of TAG accumulation, but in this plant TAG biosynthesis did not seem to compete with starch biosynthesis unlike in Arabidopsis (Zale et al. 2016). WRI1 is post-translationally regulated through phosphorylation by KIN10 kinase, which is inhibited by increasing levels of sugar, and the phosphorylated WRI1 is targeted for proteolytic degradation (Zhai et al. 2017a, Zhai et al. 2018). Other aspects of WRI1 protein stability have been described, such as a C-terminal PEST motif rich in proline (P), glutamic acid (E), serine (S) and threonine (T) that leads to destabilization of the protein, and upon removal of the motif to an increase in oil accumulation (Ma et al. 2015). Because storage TAG biosynthesis involves multiple steps across multiple organelles, the full complexity of this process is not yet understood, and much can must still be learned to realize the full potential of oil production in plant seeds.

The balance of eukaryotic and prokaryotic lipid species in Arabidopsis seems to be carefully regulated leading to a finely tuned cellular lipid homeostasis. However, many questions remain about the mechanism by which plants maintain their lipid and acyl composition. For example, it seems likely that there are mechanisms that sense membrane fluidity, acyl saturation levels and membrane curvature. What are these mechanisms? Some enzymes appear to be sensitive to their membrane environment, providing a potential layer of regulation. For example, though DAG is the preferred substrate for MGD1, the presence of PA and PG appears to be required for MGD1 membrane association and activity (Dubots et al. 2010, Sarkis et al. 2014).

Aside from regulation of bulk lipid biosynthesis, some work has been done showing how the degree of plant lipid saturation can be controlled by temperature. The Arabidopsis ω -3 fatty acid desaturase FAD8, one of two isozymes present, was shown to be post-translationally regulated through destabilization of the C-terminus when the *fad7fad8* double mutant producing a Myc-tagged FAD8 fusion protein was subjected to increasing temperature (Matsuda et al. 2005). More recently, the temperature-dependent stability of ER-localized desaturase FAD3 was shown to be linked to the ubiquitin-proteasome-system, where *B. napus* and *V. fordii* FAD3 genes were expressed in yeast and their respective protein levels were modulated by a PEST-like domain at the N-terminus (O'Quin et al. 2010).

Lipid Signaling and Response to Stress

Lipids are not only integral to the membrane architecture, but they also play an important role in signaling during growth and

in times of stress. There is a growing body of work on PA and its role in signaling in response to various cellular conditions. PA and phospholipase D (PLD), which releases PA from other phospholipids, have been implicated in a variety of stress responses by modulating enzyme activity and protein location (Wang 2005, Ruelland et al. 2015). As in mammalian systems where lipids are found in the bloodstream bound to proteins, PA and other lipid-binding proteins have been identified in the phloem exudates of Arabidopsis (Guelette et al. 2012, Barbaglia and Hoffmann-Benning 2016) suggesting long-distance movement of lipids through the plant vasculature. In mammalian cells, the importance of PA is apparent through its regulation of small GTPase-activating proteins thereby modulating the activation of Ras signaling pathways (Zhang and Du 2009). Myeloblastosis (MYB) transcription factors interact with PA and their location is influenced by lipid binding. For example, PLD has been implicated in ABA-coordinated stomatal closure, where the PLD product, PA, binds and modulates activity of ABI1 and sphingosine kinases (Zhang et al. 2009, Guo et al. 2011, Guo et al. 2012). Furthermore, much like negative feedback regulation of other pathways, PLD α 1 producing PA as a product of its lipid hydrolysis has been shown to be itself inhibited by a PA-bound regulator of G-protein signaling, RGS1, which is a GTPase accelerating protein (Roy Choudhury and Pandey 2017). The role of G-protein signaling is well known in mammalian systems, and plant G-protein signaling is becoming better understood (Pandey 2017). As more PA-regulated signaling pathways emerge, it is important to begin investigating the mechanisms by which key regulatory enzymes come directly into contact with PA and are regulated by it. Which pools of PA contribute to signaling? Is there negative feedback regulation of the lipid biosynthetic machinery by PA? Is PA or are other lipids critical for enzymatic function of lipid biosynthetic enzymes?

Another emerging area of lipid-based regulation of cellular processes focuses on the tight interplay between lipid homeostasis in the plastid and oxylipin biosynthesis. Jasmonic acid (JA), a potent oxidized lipid signaling molecule, is derived from α -linolenic acid in the chloroplast and is active in numerous developmental stages of plant growth as well as involved in responses to stress and herbivory (Howe et al. 2018). Since JA is lipid-derived, various hypotheses exist regarding the identity of the acyl-donating lipid as well as the lipases, which release the α -linolenic acid. However, while the exact molecular mechanism has not yet been elucidated, several lipid mutant phenotypes suggest that particular perturbations of plastid lipid metabolism lead to JA biosynthesis. An interesting example is the *dgd1* mutant, which is producing only small amounts of DGDG and as a result, the predominant galactolipid species present in the mutant plant is MGDG and the mutant is severely stunted in growth (Dörmann et al. 1999). Previously, it was speculated that DGDG was so important that its reduction in content alone would slow down the growth of the plant. However, when crossed with the JA-insensitive mutant *coi1*, the growth phenotype was rescued (Lin et al. 2016) showing that a disruption in galactolipid biosynthesis also disrupts JA homeostasis leading to the observed growth phenotype. Aside from changes in overall lipid content, JA accumulation has been

shown to be triggered by thylakoid-localized lipases (Wang et al. 2018), Plastid LIPases 2 and 3 (PLIP2, PLIP3). The expression of the respective genes is responsive to abscisic acid and the lipases have specificity for PG and MGDG. Thus, the roles that chloroplast membrane lipids and their specific lipases in JA signaling are playing are beginning to come into focus.

A more global plant response to stress is the remodeling of membrane lipid composition. An example is the production of oligogalactolipids during freezing in *Arabidopsis*. During freezing conditions, the activity of SENSITIVE TO FREEZING2 (SFR2) is induced, resulting in the accumulation of oligogalactolipids serving a protective role (Moellering et al. 2010, Moellering and Benning 2011), since the *sfr2* mutants are more sensitive to freezing (Warren et al. 1997). The activity of SFR2 is induced by divalent cations possibly leaking from the chloroplast as a result of membrane disruption in combination with cytosolic acidification during freezing stress (Barnes et al. 2016).

Spatial Arrangement and Complexes of Lipid Biosynthetic Enzymes

Because changing environmental conditions demand an adjustment of the extent and composition of membranes and the production of lipid-derived signaling compounds, the lipid metabolic machinery must rapidly adjust as well. Much is known about flux through the major lipid biosynthetic pathways, as well as the participating enzymes. However, a knowledge gap remains in understanding the spatial arrangement of lipid enzymes and their protein interactome. The best described lipid complexes are the ACCase, the fatty acid synthase and the TGD complex. While transport of lipids can refer to their inter-compartment movement, the movement of lipids between enzymes located on opposite sides of the same membrane, as well as the translocation of polar lipids between the two leaflets of adjacent membranes needs to be considered as well. For example, plastid PA is formed on the stromal side of the IEM (Xu et al. 2006) and MGDG assembly occurs on the leaflet facing the intermembrane space as MGDG synthase is peripherally associated with the intermembrane leaflet of the IEM (Xu et al. 2005, Rocha et al. 2016). Given this topology, one has to predict that there is a mechanism that can move PA from the stromal side of the IEM to the leaflet facing the intermembrane space where the PA phosphatase is presumably located. It should be noted, that the PA phosphatase has not been definitively localized to a certain leaflet, but its activity is found in the inner membrane and free magnesium ions in the stroma would inhibit a stromal facing phosphatase (Malherbe et al. 1992, Block et al. 1983), suggesting its location at the intermembrane leaflet of the IEM.

While most of the genes encoding lipid biosynthetic enzymes are known, there is little knowledge on the assembly of the respective proteins into higher order complexes. Plant desaturases appear to function as dimers, with a crystallized di-iron Δ^9 -desaturase of castor bean providing an example (Schneider et al. 1992, Lindqvist et al. 1996). Recently, the first plant acyl-CoA binding protein structures were solved using

rice homologs OsACBP1 and OsACBP2 (Guo et al. 2017). The structure of MGD1 synthase has been described, as well as its PA binding properties (Rocha et al. 2016), though we do not know of any higher oligomeric states. It has been hypothesized that enzymes such as DGD1 and the TGD complex, which also bind PA, could be aggregating as a result of PA binding (Kelly et al. 2016). Though just a hypothesis, these insights pose interesting questions about the mechanisms of regulated oligomerization and possible substrate channeling by lipid enzymes. Moreover, while more data are being collected on enzymatic activities and physiological roles of lipid biosynthetic proteins, the majority of lipid enzyme structures remain to be solved.

Overall, more biophysical information is needed on lipid biosynthetic enzymes in order to create accurate models of plant lipid metabolism, identify mechanisms of regulation, and ultimately optimize biofuel and food crops for oil accumulation. Numerous efforts have been made to catalog and characterize the proteome of plant cells, including chloroplasts (Ferro et al. 2003, Froehlich et al. 2003, Breuers et al. 2011, Lundquist et al. 2017). With this basic information available, the plant lipid community is slowly beginning to assemble the 3D landscapes of our current 2D models depicting lipid metabolism.

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The authors have no conflicts of interest to declare.

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